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RESEARCH

Ecology of a brushtail possum (*Trichosurus vulpecula*) population at Castlepoint in the Wairarapa, New Zealand

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Abstract: Brushtail possums at a 21 ha site at Castlepoint in the Wairarapa, New Zealand, were studied with capture-mark-recapture from August 1989 to August 1994. The mean annual adult population density, based on counts of mature possums trapped each year, was 8.7 per ha and varied by only small amounts during the study period. The median survival age was 32 months (95% CI 28–39) for females and 27 months (95% CI 26–30) for males. Mean body weights were 2.47 kg (95% CI 2.46–2.49) for mature male possums and 2.34 kg (95% CI 2.32–2.36) for mature female possums. Body weights were lowest in autumn–winter, increased during spring and were highest during summer in each year. Breeding started in March each year and there was a secondary pulse in spring. No births were recorded in the summer. The median age for time to first successful mating for females was 14 months and almost all females bred each year. Rates for successful breeding in both autumn and spring ranged from 100% for the 90th percentile to 56% for the 10th percentile. The population contained more males than females throughout the study period but depopulation data showed a predominance of males in the age group of up to 4 years and similar proportions thereafter. The outstanding features of this population were its high density, high fecundity, breeding at an early age and a short life expectancy. It illustrates the widely varying location-specific performance of the species. Known causes of death included tuberculosis, iatrogenic haemopericardium and exposure–starvation. Juvenile possums often used dens that appeared to give poor protection during rain and cold conditions, and our observations suggest that a lack of dens which could provide protection from adverse weather was probably more important than abundance of food in regulating population density in the ecological setting at Castlepoint.

Keywords: body weight, brushtail possum, ecology, mortality, reproduction, *Trichosurus vulpecula*

Introduction

The importance of the brushtail possum, *Trichosurus vulpecula*, as an introduced pest in New Zealand and its asset value in its native Australia have given it priority among naturalists as a subject for research. Despite this research, most of the studies in New Zealand have been cross-sectional and only two longitudinal capture-mark-recapture studies covering multiple generations and of 4 or more years' duration have contributed via peer reviewed publications to our understanding of possum demography; the ongoing Orongorongo Valley studies commenced in 1966 (Crawley 1973) and the 4-year Turitea study in 1996 (Ramsey et al. 2002). The Orongorongo Valley study's original aim of long-term monitoring of the impact of introduced mammals on native forest was subsequently expanded to more intensive ecological studies of the possum population (Crawley 1973; Bell 1981; Efford 1991) and more recently to effects from the introduction of tuberculosis caused by *Mycobacterium bovis* (Ramsey & Cowan 2003; Arthur et al. 2004). Possum density is dependent on habitat type (Efford 2000) and the insights into the demography and population dynamics of the Orongorongo Valley and Turitea resident populations reflect the forest habitat for both of those sites. Information for other habitats largely comes from multiple cross-sectional studies, which despite their value for inference, are unable to fully capture temporal and spatial changes.

This paper derives from a study of a *M. bovis* infected population in a scrubland pasture setting at Castlepoint in the

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Wairarapa region of New Zealand (Pfeiffer & Morris 1991) which ran from 1989 until 2000. The data were collected by a group of PhD and Masters students engaged in a research programme conducted by the EpiCentre at Massey University aimed at understanding how infection with *M. bovis* was maintained in wild possum populations and the role of possums in transmission of the disease to cattle and other species. The paper describes aspects of the structure and population dynamics of the study population and the ecological setting for its endemicity with *M. bovis*. The objectives for the first 65 months (April 1989 to August 1994) of the study programme were investigating the epidemiology of naturally occurring *M. bovis* tuberculosis in possums, modes of transmission of the disease from possums to cattle and production of data and statistics for incorporation into simulation models of the disease (Pfeiffer 1994). We use data from those first 65 months and during depopulation in August to October 1994 to describe the ecology of possums at the Castlepoint study site, emphasising the dynamics and temporal variation of the population, survival, breeding success, and individual growth patterns. Where appropriate, we briefly discuss some of the differences between aspects of the performance of this population and those reported from other longitudinal studies in New Zealand (Bell 1981; Efford 2000; Cowan 2005) and Australia (Isaac 2005).

The paper is intended to add to the extensive literature regarding reproduction and ecology of brushtail possums in New Zealand, which has been comprehensively reviewed by several authors (Efford 2000; Fletcher & Selwood 2000; Ramsey et al. 2002; Caley & Hone 2004; Cowan 2005). It also responds to a plea by Caley (2006) for more documentation in peer reviewed publications of information about possum populations, and in particular those which are infected with tuberculosis.

Methods

Study site

The 21 ha study site (40° 50′ 45.87″S, 176° 13′16.39″E) (see Appendix S1 in Supplementary Material) near Castlepoint on the Wairarapa coast of the North Island of New Zealand was located in a sheep and beef cattle farm of approximately 1000 hectares that was still under development. The study site was selected because possums were plentiful, tuberculosis had been diagnosed in possums and cattle in that part of the farm, it was located at the back of the farm and the owner was willing to allow a long-term study there. Although extensive clearing of predominantly mānuka scrub (*Leptospermum scoparium*) occurred in the 1970s to establish pasture, indigenous scrub and regenerating forest had persisted in some of the steeper gullies and occurs in patches throughout the farm. The paddocks containing the study site were partially cleared of mānuka, which was pushed into piles of residual timber (root rakings), and the paddocks were intermittently grazed by cattle. Rough, largely exotic grassland was established in the clearings on the slopes and the valley floor but artificial fertiliser was never applied. Water was plentiful in creeks and gullies throughout most of the year except in seasonally dry summer periods. Possums were not subject to any controls apart from occasional spotlight shooting on the valley floor. Tuberculosis was known to occur in possums and cattle in the valley.

The southern portion of the site was on the sunny side of the valley and was consequently drier than the northern shady side. The predominant vegetation on the southern and eastern side was an open shrubland of mature mānuka interspersed with mixed small shrubs, and with some gorse (*Ulex europaeus*) along the south-west boundary. Pasture was plentiful in small clearings. Flax (*Phormium tenax*) was absent on the southern side. The predominant species on the steeper northern side was a mixed scrubland of mānuka and other broadleafed ‘pioneer’ trees such as mahoe (*Melicytus ramiflorus*) and kanono (*Coprosma grandifolia*), as well as the tall black tree fern or mamaku (*Cyathea medullaris*), characteristic of slightly moister habitats, with a well-developed understorey, including a rich fern flora. Large mature flax plants were common and mingimingi (*Leucopogon fasciculatus*) and *Coprosma rhamnoides* were plentiful in the understory. Gorse was plentiful along the northern boundary, which was also partially marked by a row of mature pine (*Pinus radiata*) trees. Thus, there was a wide variety of food trees and shrubs available to possums. Palatable plants include hangehange (*Geniostoma rupestre*), mahoe, lacebark (*Hoheria sexstylosa*), rangiora (*Brachyglottis repanda*), mamaku (*Cyathea medullaris*) and several *Asplenium* species. There were small well-pastured clearings throughout. A gully with a high density of *Cyathea* species bounded the site on the north-west side and appeared to support a reasonably dense population of possums as judged from possum sign and evidence of browse. The two extensive properties to the north and west of the study area supported large populations of possums and were also inhabited by wild red deer (*Cervus elaphus scoticus*) and feral pigs (*Sus scrofa*) at the time of the study.

Trapping and marking of possums

A capture-mark-recapture study using treadle and trigger operated wire-mesh cage traps with a metal sheet cover at fixed locations (see Appendix S2) commenced in April 1989 and this component of the overall investigations concluded in August 1994. Up to August 1989 about 120 traps were used, after which they were increased to 295. Traps were not set in a grid but were located with regard to ease of access, existing tracks and operators’ perceptions of possum abundance. Initially, traps baited with apple dusted with cinnamon-flavoured flour were set for 5 consecutive nights at monthly intervals, except for July 1989 when the number of nights was reduced to 3 because of adverse weather. After May 1991, the number of trap nights per month was reduced to 3 consecutive nights for possum welfare, logistic and financial reasons, after trapping statistics from the 13th to the 25th month showed that 87% of known possums and 70% of previously unknown possums were captured in the first 3 nights. All trap sites were geo-referenced using a global positioning system.

Captured possums were sedated with intra-muscularly injected ketamine (Parnell Laboratories 95 New Zealand Ltd, Auckland, New Zealand) at a dose rate of 35 mg kg^{-1}. All animals were identified with a unique numbered metal ear tag, a unique ear tattoo number and a system of ear notches when first captured. After their initial capture, possums were sedated and examined every 2 months or at the first opportunity if the interval between successive captures was greater than 2 months. Exceptions were made for possums diagnosed as tuberculous which were examined every month or at the earliest opportunity. Body weight (measured to the nearest 10 mg with spring balance), body condition (good, average or poor, assessed subjectively by palpation), nose-tail and tail lengths (measured in cm with tape measure), tooth wear class based on upper first left molar, sex, presence of pouch-young (PY), evidence of lactation, coat colour, and trap location were recorded at each examination. Head length and total length, measured to nearest mm with Vernier calipers were recorded for PY, and they were identified with a small ear tag if considered large enough to have an ear tag safely applied. Sex was determined in PY with at least 12 mm head length by means of the presence of pouch or scrotum contents (Tyndale-Biscoe 1955). Maturity was recorded as either PY, immature or mature. Immatures, hereafter referred to as juveniles, were defined either as males with testicle width <14 mm or as females with no invaginated pouch. Ages in months were subsequently estimated using a combination of methods which included visual estimation from body size, testicle size and pouch development, tooth cementum layers (Pekelharing 1970) and tooth wear records (Winter 1980; Cowan & White 1989). Trap location, identity and date of capture were recorded for all captures.

Radiotelemetry using radio collars and direct observations were used to investigate the use of sleeping dens and foraging activity (Paterson et al. 1995). Radio collars were attached to all possums with clinical signs of tuberculosis and some others, based on needs to obtain information on survival of diseased possums, behaviour of dispersing juveniles and to determine extents of home ranges. On occasions when logistics permitted, radio-collars were fitted to randomly selected possums.

Depopulation of the study site commenced in August 1994 and continued thereafter during weekly trapping sessions during September and October. All possums captured during depopulation were humanely euthanised by injection with sodium pentabarbitone, and necropsied and examined for evidence of infection with *M. bovis.*

Data analysis

Population sizes of possums were estimated from counts of mature male and female possums which were trapped in each year from 1990 to 1993 and for 1994 from trapping up to August and during depopulation. Reproduction, recruitment, and survival were evaluated as additional demographic parameters for describing the overall dynamics of the population. Reproductive performance was based on the number of successful pregnancies calculated for the 65 months between 1989 and 1994. Establishment of pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a joey. The Lyne and Verhagen (1957) nomogram (Lyne & Verhagen 1957) was used to estimate birth dates of 421 individual PY of which 189 were ear-tagged before independence. Individually identified PY captured after independence are referred to as the known-as-PY-cohort (n = 124). We consider this cohort to be a relatively unbiased representation of the population, because our only influence on their selection was deciding whether an ear tag could be safely applied. The known-as-PY cohort provides information about early growth, reproductive performance and deaths. The time of the first reporting of PY depended on the time of trapping of their mothers and only PY considered large enough to have an ear tag safely applied were individually identified. For the purposes of survival analyses, possums other than the known-as-PY-cohort that entered the study as juveniles (n = 330), were allocated default birth dates of 15th April or 15th October based on body measurements. These latter possums are referred to as the estimated-birth-date-cohort.

Kaplan Meier survival function estimates plotted against time present a profile of probability of an event happening each month, given that the event was still current up to that month. The survival analyses were conducted in Stata/IC 13.1 (StataCorp LP) to determine the temporal pattern of the survival of individual possums and the age at maturity for males and females. Kaplan–Meier curves of survival time and time to maturity were generated for these events and log-rank tests were used to test the null hypothesis that survival curves did not differ between males and females. Survival function estimates for mortality were based on the known time of confirmed death, the known time of loss to follow-up, and the last time they were trapped. In the absence of evidence of death, possums were ruled right-censored if they had been trapped in the last 6 months and lost to follow-up if they had not been seen after the 59th month of the 65-month study. This compromise was chosen because the figure for known deaths was considered to be an underestimate and the one for loss to follow-up an overestimate. Possums were credited with one month's survival at their first trapping occasion, meaning that animals that were captured on only one occasion were considered to have survived for that month. Possums that died from iatrogenic misadventure were excluded from all survival analyses to remove bias from that cause.

Influences of sex and season on possum body weight and the influence of sex on the possum growth rates were explored using linear mixed-effect models, which accounted for correlation between repeated measures on individuals. One model investigated the influence of sex and season on body weight with season categorised as summer (December, January and February), autumn (March, April and May), winter (June, July and August), and spring (September, October and November). The other model investigated the influence of sex on body weight with age (Arthur et al. 2004) and sex of each weighed possum as categorical risk factors. These models were constructed using the nmle package (Laird & Ware 1982; Venables & Ripley 2002) in the statistical and graphical software environment R 2.20 (R Core Team 2005) and first-order interaction terms were retained if significant at an alpha level of 0.05.

Results

Trapping statistics

Traps were set for 67 183 trap-nights over 249 nights during 65 monthly visits from April 1989 through to August 1994. The average catch success was 0.28 (range 0.09–0.47) per trap-night (uncorrected for sprung traps). Summary information was calculated for all visits beginning at visit five, when monthly trapping effort first exceeded 1000 trap-nights, to visit 61. The number of possums sedated and clinically examined at each visit ranged from 31 to 110 (mean and median = 71). A total of 728 possums (273 females and 455 males) were captured and individually identified and a further seven previously unidentified animals were found dead at the study site during the study period. The ratio of black and grey coat colours in the study population was one black to 5.54 grey. The numbers of newly caught possums and all possums captured in each whole calendar year (1 January to 31 December) from 1990 to 1993 classified by maturity and sex are shown in Table 1. No significant differences in the proportions in each class over time were detected by χ^2 tests for newly captured possums ($\chi^2 = 9.0394$, df = 9, P = 0.434) or for all re-captured possum ($\chi^2 = 11.609$, df = 9, P = 0.236). Seven feral ferrets (*Mustela furo*) were captured as by-catch.

The numbers of individual mature males and females captured each year (with year in parenthesis) within the study

Table 1. Numbers of newly captured possums and all individual possums, stratified by maturity and sex, captured in each whole calendar year between 1990 and 1993.

Time period	Total	Juvenile females	Mature females	Juvenile males	Mature males
Number of newly captured possums					
Jan to Dec 1990	91	22	10	40	19
Jan to Dec 1991	117	26	7	69	15
Jan to Dec 1992	99	24	10	50	15
Jan to Dec 1993	103	26	13	53	11
All captures					
Jan to Dec 1990	268	38	82	52	96
Jan to Dec 1991	278	32	66	78	102
Jan to Dec 1992	280	34	66	64	116
Jan to Dec 1993	295	35	82	60	118

site were 178 (1990), 168 (1991), 182 (1992), 200 (1993) and 186 (1994). The number of mature possums for 1994 was derived from trapping data during depopulation. The average number of mature possums that were known to frequent the study site for the whole period was 183, giving an average estimated population density for the whole period of 8.7 mature possums per hectare.

During the period from July 1989 to July 1993, radio-collars were attached to 147 possums, enabling tracking to a total of 595 den sites on 818 occasions. Individual possums were tracked from one to 44 times (mean = 5.6) and from one to 32 separate dens (mean = 4.6). There was a strong correlation (Pearson's correlation coefficient $r = 0.98$) between tracking effort and the number of separate dens recorded per possum. Between January 1991 and July 1993, the type of den used and the weather (rainfall, cloud coverage, temperature) on the day of tracking as well as on the day prior tracking were recorded. In that 30-month period, 67 possums were tracked on 358 occasions to 281 separate dens and individual animals were tracked from one to 23 times (mean = 5.2). Den sharing outside of the mother-offspring relationship was recorded on two occasions. Of the 281 dens, 133 (47%) were located under flax plants, 45 (16%) in bulldozed heaps of mānuka root-rakings formed during scrub clearing, 39 (14%) in gorse, 24 (9%) in long grass shelters, ten (3%) in *Pinus radiata* trees, eight (3%) in underground burrows, six (2%) in mamaku, one in a cabbage tree (*Cordyline australis*) and the remaining 15 (5%) in miscellaneous locations. One root-raking den was occupied on separate occasions by three different possums and 13 other dens (four flax, five root-raking, one burrow, one pine tree and two gorse) were twice used on separate occasions by different individuals. Many of the root-rakings were large (up to 6 m by 3 m) and contained extensive connecting tunnel-like spaces. No associations were found between the type of den occupied and weather, either on the day of tracking or on the previous day.

Deaths

Deaths as a result of blood collection, starvation–exposure and tuberculosis

A total of 4427 blood samples were collected by cardiac puncture from 708 possums as part of the tuberculosis component of the study. On 69 occasions (average risk = 0.016 death per blood sampling event) possums were known to have died from haemopericardium produced by haemorrhage into the pericardial sac during blood collection by cardiac puncture. The incidence of haemopericardium was probably higher than was detected because organised blood clots were occasionally found in the pericardial sacs of possums that died from other causes and some deaths due to haemopericardium may not have been observed. Individual possums were bled an average of 6.25 times (range 1–32), females 6.7 (range 1–32) and males 6.3 (range 1–32). Proportionately more females died than males (35 of 265 *vs* 34 of 443; risk ratio = 1.72, 95% CI 1.1–2.7).

Deaths from disease or other natural causes

Post mortem examinations were conducted on all possums that were found dead or were euthanised because they were debilitated and in extremis. Tuberculosis, confirmed by culture or gross pathology, was responsible for 66 deaths; and starvation–exposure, based on poor body condition, low fat reserves and signs of adrenal exhaustion, for 41.

The median survival age of the 652 possums (236 females and 416 males) eligible for survival analysis was 29 months (95% CI 27–31; Fig. 1). The median survival age was 32 months (95% CI 28–39) for females and 27 months (95% CI 26–30) for males, and the log-rank test showed significant differences between the survival functions. Survival curves (Fig. 1) show about 25 per cent of male and female deaths occurred in the first 15 months with similar rates for both sexes up to that age and different rates thereafter.

Reproduction

(a) Overall breeding activity

The overall distribution of births by calendar month is shown in Figure 2. Given a gestation length of approximately 18 days, breeding commenced in March of each year, following a period of no breeding activity that extended at least through December to February in all years. No births were recorded during those summer months and the four births recorded in March were estimated to have occurred in the last week of the month. The main breeding pulses occurred regularly each autumn with secondary phases of activity in spring. Throughout the study period, testicular tone (degree of firmness of the testicles felt during palpation) in mature males was noticeably increased at the times of onset of pulses of female breeding activity (pers. obs. RJ and BMP). See Appendix S3 in Supplementary Material for summary statistics of seasonal distribution of

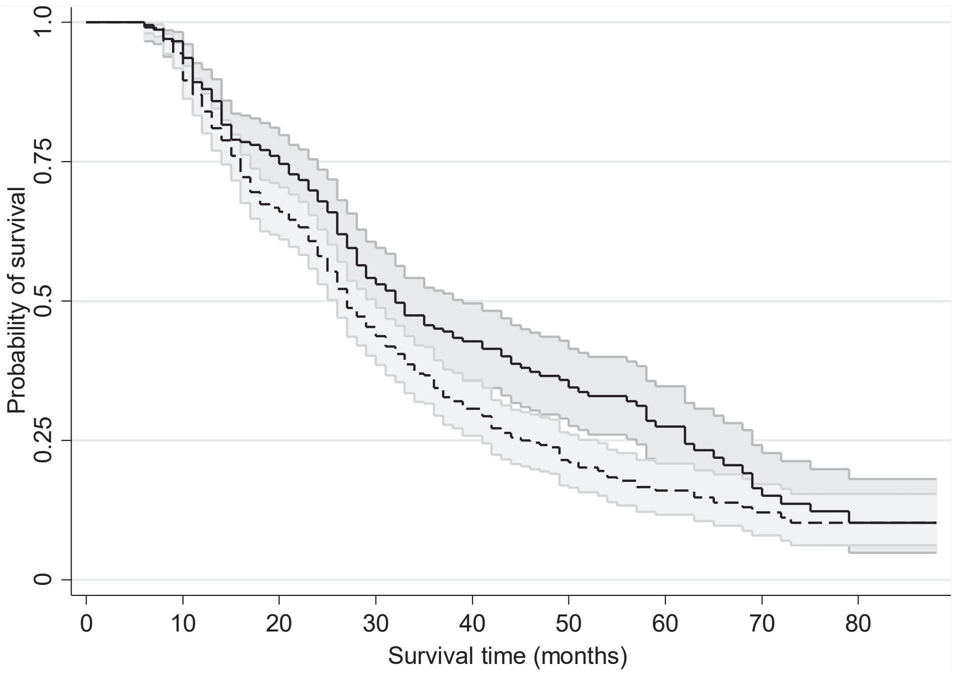


Figure 1. Kaplan-Meier survival curves with 95% confidence intervals for time to death from disease or other natural causes for 236 female (solid line) and 416 male (dashed line) possums.

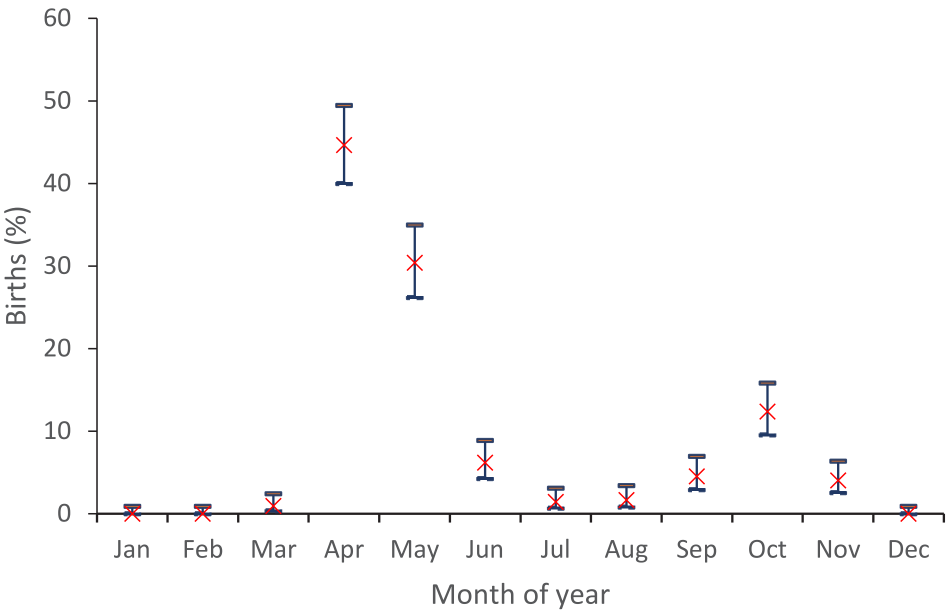


Figure 2. Percentages (×) and 95% confidence intervals (−) of births by calendar month occurring in the possum population at Castlepoint between April 1989 and August 1994.

numbers of successful matings and median and mean dates for successful matings 1989–1994.

At visits during June 1990, June 1991, June 1993 and August 1994, all mature females examined had PY. In 1989 and 1992, 86% and 95% of mature females had PY respectively. The overall average monthly temporal pattern of proportions of captured mature females with PY or evidence of lactation to all mature females that were captured is shown in Figure 3.

(b) Age at sexual maturity

The time of first successful mating, defined as one which resulted in a PY, was recorded for 30 (56.7%) of 50 female possums in the known-as-PY-cohort which were eligible for analysis. The temporal pattern in the Kaplan-Meier survival curve (Fig. 4) illustrates the onset of sexual maturity for those 30 females. The youngest age at first successful mating was 10 months and the median was 14 months.

In contrast, the earliest recorded age for a male possum to reach sexual maturity was 14 months. The distribution of numbers of juveniles and mature males at ages ≥14 months is shown in Table 2. The records for male maturity are conservative, because unlike the data for females where ages of PY could be established from PY head length, the time at which males were first reported to be mature was dependent on measurements made at their time of capture.

One male which entered the study in 1991 at 12–18 months of age and was regularly examined until August 1994 failed to achieve ≥14 mm testicle size. Its maximum testicle size was 12 mm and its maximum body weight was 2.1 kg. No histological examination of the testes was made and it is not known if this animal was fertile or sexually active.

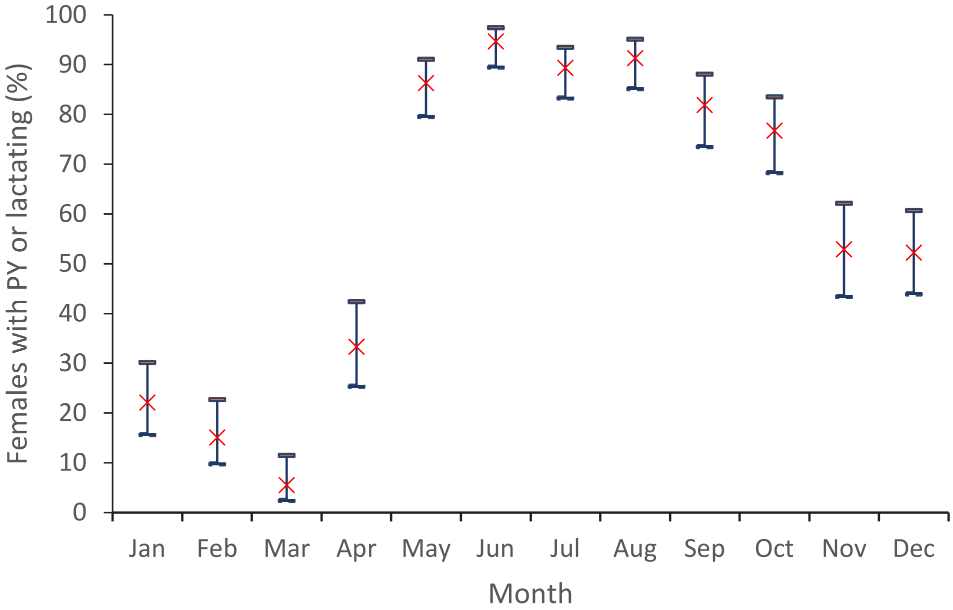


Figure 3. Monthly temporal pattern of point estimates (×) and 95% confidence intervals (⊖) of percentages of captured mature females that had pouch-young or evidence of lactation.

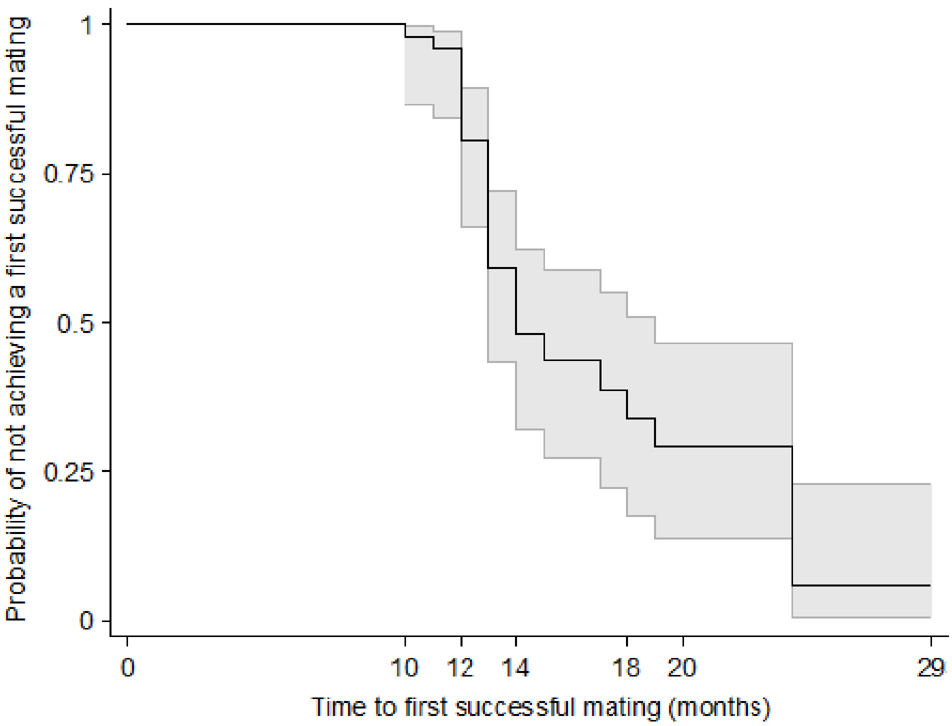


Figure 4. Time to maturity. Kaplan-Meier survival curve with 95% CI (shaded) for time for female possums in the known-as-PY-cohort reaching sexual maturity. Maturity was defined as age at first successful mating.

Table 2. Numbers of sexually mature and juvenile male possums recorded at ages ≥ 14 months.

Age (months)	Mature	Juvenile
14	1	1
15	1	2
16	2	8
17	5	5
18–29	9	0
Total	18	16

(c) Multiple successful breeding episodes

The 124 known-as-PY possums were the offspring of 73 individual female possums. Of 29 females in the known-as-PY cohort that subsequently bred, 15 had one, eight had two, three had three, one had four, one had five and one had six offspring. One-hundred and seventy-three female possums had PY during the study period, and of these 101were known to have bred more than once (range 2–8 times). The probability of breeding for mature females in the autumn and spring breeding season were calculated for 90 animals for which continuous seasonal data were available and ranged from 0.3 to 1.0. Possums in the upper 10th percentile bred successfully every autumn and spring breeding season whereas those in the

Table 3. Percentile distribution of the rates (with 95% confidence intervals in brackets) for individual female possums having a successful breeding episode for every autumn and spring breeding season during the period when she was mature and for which continuous seasonal data were available (n = 90).

Percentile	10th	25th	50th	75th	90th
Rates	0.56 (0.4–0.6)	0.6 (0.6–0.67)	0.67 (0.67–0.73)	0.84 (0.8–1.0)	1 (1–1)

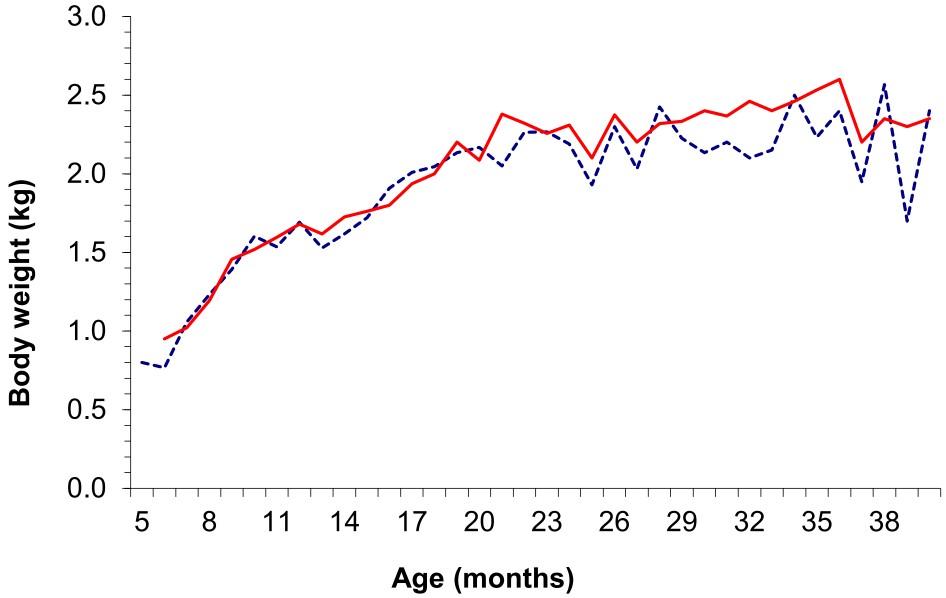


Figure 5. Temporal pattern of average body weights in kilograms of known-as-PY males (red solid line) and female (blue stippled line) from independence to maturity (n = 124).

bottom 10th percentile bred successfully in both spring and autumn in 56% of seasons (Table 3).

There was no evidence to suggest that any possums were naturally barren. One possum that entered the study in 1989 as an adult and bred in October 1989 showed no further evidence of breeding to her death at about 5 years of age from natural causes in December 1992. Three possums that were examined regularly through to their first breeding episode, which resulted in an observed PY, did not breed until >700 days (709, 730 and 732 days).

(d) Rearing to independence

It was not possible to determine the proportion of breeding episodes that culminated in successful rearing of offspring to independence because some PY were not tagged and some tagged PY were not recaptured.

Body weight

(a) Growth rates

The temporal pattern of growth rates from independence to maturity were similar for males and females in the known-as-PY cohort (Fig. 5).

Growth rates up to independence were similar for all males and females in the study population and although increasingly sparse data at older ages do not allow firm conclusions to be drawn, males showed a strong seasonal variation of weight from 30 months on (Fig. 6). Females, however, presented a more regular growth pattern with less marked seasonal weight changes. After adjusting for logarithmically scaled ages and repeated measures on individuals, males were on average 71 g (95% CI 36–106, $P < 0.001$) heavier than females over their lifetime.

(b) Seasonal changes in body weight

Over the entire population, adult possum body weights ranged from 1.5 to 4.0 kg and 1.3 to 3.6 kg for males and females, respectively. The mean body weight was 2.47 kg (95% CI 2.46–2.49) for mature male possums (n = 287) and 2.34 kg (95% CI 2.32–2.36) for mature female possums (n = 204) (including any PY). Body weights of both sexes declined regularly in autumn–winter and were highest during the summer months in each year (Fig. 7).

Body weight records (n = 3368 from 468 possums) from females at ages >15 months and from males >18 months were used to calculate a season- and sex-adjusted mean body weight of 2.3 kg (95% CI 2.28–2.38). Males were heavier than females by an overall average of 224 g (95% CI 162–285). Possums were significantly lighter on average in spring and winter by 106 g (95% CI 74–138) and 34 g (95% CI 3–65) respectively than in summer. There were no significant differences between summer and autumn body weights ($P = 0.24$). Males appeared to be more affected than females (uncorrected for PY) by seasonal changes, with average body weight losses of 114 g (95% CI 72–156), 247 g (95% CI 205–288) and 123 g (95% CI 81–166) in autumn, winter, and spring, respectively.

Profile of the study population at final depopulation

A total of 107 males and 79 females that had been previously identified and tagged were captured and necropsied at the end of the study in August to October 1994. Years of birth for 43 possums which were known as PY and estimated ages for the remainder (see Methods) were used to construct an age profile of the depopulated study population (Fig. 8). The mean and median ages were 39 and 41 months for males and 46 and 42 for females and there were more males than females in

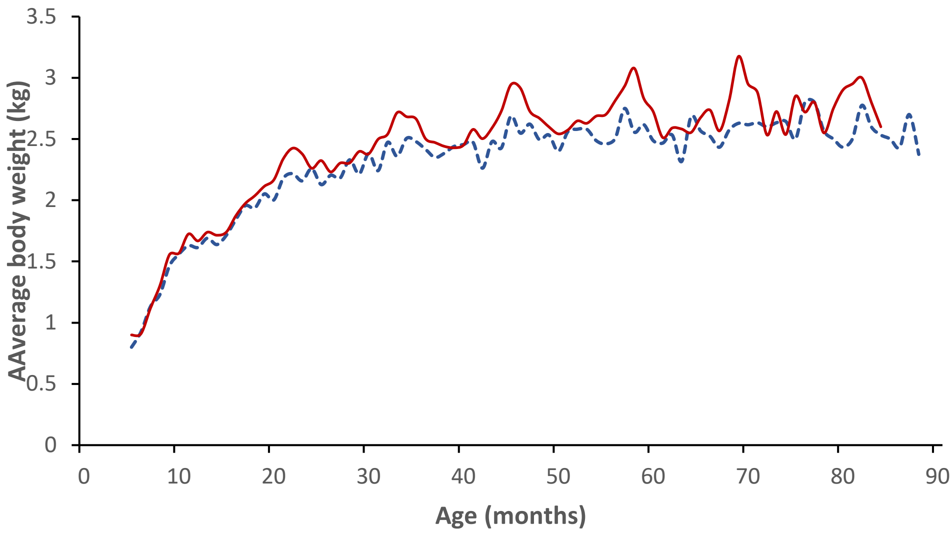
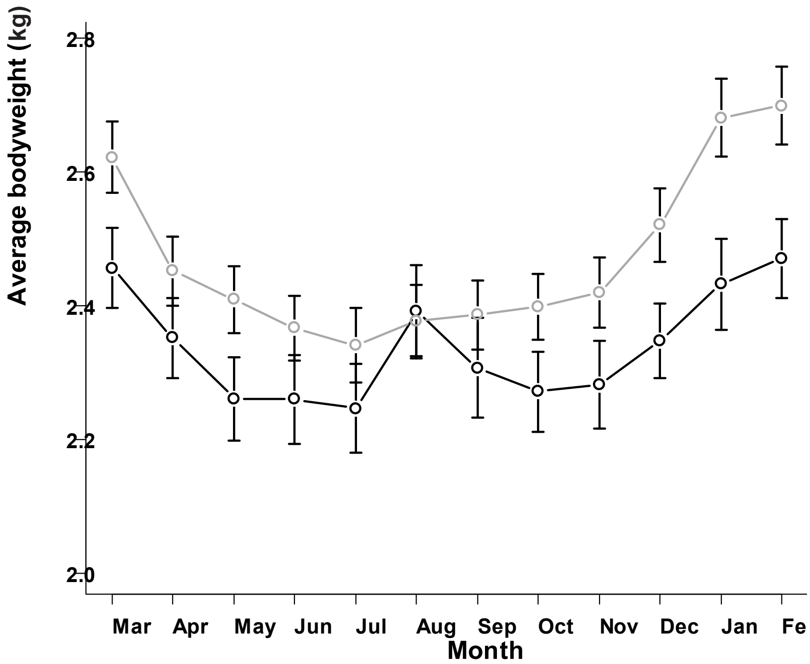


Figure 6. Temporal pattern of average body weights in kilograms of all males (red solid line) and females (blue dashed line) from independence to 90 months of age.

Figure 7. Temporal pattern of average body weights of adult male (upper grey line) and female (including any PY; lower black line) possums. Bars represent 95% confidence intervals.



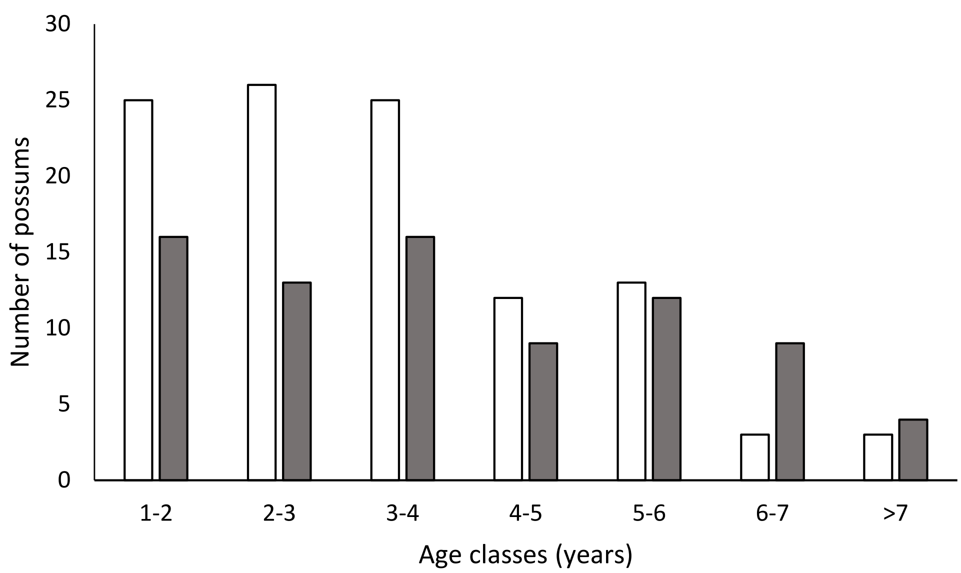


Figure 8. Distribution of known or estimated ages of previously identified female (■) and male (□) possums trapped during depopulation of the study population.

the age classes up to 3 to 4 years but little difference beyond that. Of the 79 females, seven were juvenile and evidence of pregnancy from presence of PY or lactation was not recorded for 10 mature females trapped on an adjacent property by a professional trapper. Evidence of pregnancy was present in 60 of the remaining 62 females for which data were recorded.

Discussion

This study offers insights into the performance of the study population at Castlepoint over 65 months of observation. Longitudinal studies of wildlife are difficult to implement and are relatively rare compared to cross-sectional studies. However, their data are more complete and offer more opportunities for generation of hypotheses about factors that influence performance. The outstanding features of this population were its high density, high fecundity, breeding at an early age, short life-expectancy and denning at ground level (cf. review by Cowan 2005). The study further illustrates the widely varying location-specific performance of *Trichosurus vulpecula* described in other studies (Brockie 1991; Coleman & Green 1984; Ramsey et al. 2002; Isaac 2005) and in this paper.

Trapping statistics

An important consideration for capture-mark-recapture studies is the efficacy of the trapping effort for identification of the animals that frequent the study site. The large number of traps employed (295) and the intensity of trapping during 3 nights in every month were designed to optimise capture probability. We consider our estimates of numbers of adult possums known from trapping to frequent the study site in each year to be reasonably robust and they are supported by a comparable count at depopulation. The mean adult population density based on these estimates was 8.7 per ha and annual estimates varied little during the study period, indicating a reasonably stable population size. However, these estimates do not consider increases in the summer from captures of newly recruited juveniles after independence along with immigrants from adjacent populations and declines during the colder months due to emigration and increased risk of death from starvation–exposure.

Deaths

We are aware of no other study of possum survival based on Kaplan-Meier analysis, and most measure survival in years instead of in months as we did. The actual median survival times may have been shorter than our estimate (32 months for females and 27 for males) because the dataset for survival analysis only contained 118 PY that were individually identified after they were independent. The fate of 65 PY that were identified and not captured after independence is unknown; they may have survived and not been captured or they may have died. Predation by feral ferrets (captured as by-catch) may have contributed to deaths of young possums.

In addition, it is likely that many more deaths resulted from starvation–exposure than the 41 identified, because many carcasses would not have been found. The 69 known deaths from cardiac blood collection were an unfortunate consequence of the relatively large volumes of sera required for our attempts to develop a serological test for tuberculosis that would enable calculation of reliable estimates of incidence, time of initial infection and time to death.

Fecundity

The population exhibited a high level of fecundity with most females breeding in their first year of independence, with almost all females breeding each autumn, and some also giving birth in the spring. No births were recorded in the summer months. We consider the known-as-PY females that were eligible for Kaplan-Meier analysis of time to first successful mating to be a reasonably unbiased representation of females entering the population but only 30 possums were included in this analysis and the 95% confidence intervals for the survival curve (Fig. 4) reflect the uncertainties for the estimates. Our median age of time of first successful mating of 14 months would be reported as 2 years if time intervals of years were used and our use of months for time periods in the analysis provides a better appreciation at a finer resolution of the temporal pattern of onsets of first successful mating than would come from using year time intervals. The temporal onset of sexual maturity in males, as judged by testicular size, was slightly later than the timing for first successful mating in females and increases in testicular tone coincided with normal seasonal changes in the reproductive tracts of adult males in the breeding seasons (Fletcher & Selwood 2000).

Body weight, seasonal changes and sex ratio

Adult body weights were similar to those at other locations in the North Island of New Zealand, with adult males heavier than adult females (Cowan 2005). Body weights showed a regular decline in each autumn–winter, an increase during spring and highest weights in summer.

Capture data indicated more males than females in the population, but stratification of ages at depopulation showed a predominance of males in the age classes of up to 3 to 4 years but similar proportions thereafter. This observation is consistent with earlier findings by Coleman and Green (1984). Males at Castlepoint had larger activity ranges than females (Paterson et al. 1995) and it is likely that overlapping males from contiguous populations contributed to the imbalance.

Population stability

The relative stability of the study population over time is intriguing and suggests that environment and habitat-related factors play a large part in its regulation. A replacement rate that would balance the constraints of short median survival times (27 months for males and 32 for females) was required to maintain the population. We propose a high level of mortality from natural causes from around independence to about 18 months of age as a contributing factor for maintenance of that stability. Possums at the study site denned mainly at ground level and few dens (6%) were located above ground in trees or mamaku fern crowns. In other studies, most possums denned in trees, but ground-level dens were common in some locations (Cowan 2005). Juvenile possums at the study site often used dens, such as in grass sheltered only by low ferns, which frequently had damp or wet floors that appeared to provide poor protection from adverse weather (Paterson et al. 1995) and those authors reported nine of 25 juveniles died within 10 months of tagging. Newly independent possums, in particular, would be at serious risk of exposure–starvation if they do not have access to dens with adequate shelter from rain and cold during periods of bad weather, in addition denning at ground level allows easy access for predators such as ferrets. Possums are close to the lower limit of body size for herbivores and their small body size and relatively large surface area makes them prone to energy loss through the skin. They are reluctant to leave dens when it is raining (Ward 1978) and their fur coat is not waterproof. Conditions of cold wet weather, dens with inadequate protection of occupants from rain and cold, reluctance to forage when it is raining, and declining nutritional value of foods may contribute to the weight losses observed for adults during winter and could conceivably put susceptible possums at risk of death from starvation–exposure. Juvenile possums are likely to be at the greatest risk because of their energy needs for maintenance and growth, for finding shelter from rain and cold, and competing with established older residents for home range, food and shelter.

The site-specific population dynamics of possum populations is illustrated by the contrasts between the Orongorongo and Castlepoint populations. Estimated possum density was similar or slightly higher at Orongorongo (mean of 9.2 per ha (Efford 2000) *vs* 8.7 at Castlepoint), but fecundity there (Bell 1981; Green 1984) was much lower and more variable. The early maturity and high fecundity, which were notable features of the Castlepoint and another farmland related population (Brockie et al. 1997), indicate an adequate food supply and growth and reproductive performance not constrained by poor nutrition. Our observations suggest that availability of dens offering adequate protection from adverse weather was probably more important than abundance of food in regulating population density in the ecological setting at Castlepoint, contrasting with the reverse proposal (Green 1984) for food resources being more important than den site availability in most of New Zealand.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Photo of the study site.

Appendix S2. Topographical map of the study site showing all 295 trap locations.

Appendix S3. Tables showing the seasonal distribution of birth dates for each year and median and mean dates for each autumn and spring.

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